

RELATIVE EGG SUCCESS AND IMPLICATIONS FOR  
DISTRIBUTION OF THREE SYMPATRIC MANTIDS  
(MANTODEA: MANTIDAE)

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*Abstract.* — We compared hatching success and mortality of eggs among three sympatric mantid species (*Tenodera aridifolia sinensis* Saussure, *T. angustipennis* Saussure, *Mantis religiosa* Linnaeus) in two field sites in northern Delaware. Oothecae were heavier in CHRY than AG (two old-field study sites) for all three species, indicating a difference in feeding opportunity for adults in the parental generation. However, hatching success did not differ between sites, so that adult feeding condition did not affect the probability of successful emergence of the next generation. None of the egg mortality for any species was caused by natural enemies in these populations. Hatching success was dramatically lower for *M. religiosa* than for the two *Tenodera* species, reflecting a difference in tolerance to abiotic environmental factors.

*Key Words:* Egg ecology, Mantodea, Mantidae, *Mantis*, *Tenodera*, oothecae, predators

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Nymphal production by a number of mantid species has been reported in the literature (Girault 1907, Rau and Rau 1913, Laurent 1913, Weiss 1914, Bromley 1932, Roberts 1937, Fox 1939a, b, Eisenberg and Hurd 1977, Matura 1979, Matura and Morooka 1983). However, only Fox (1939a) and Eisenberg et al. (1992) compared egg hatching success between species or sites. Such comparisons are of value, because they may indicate differences in suitability of the environment within and between geographical regions as well as among species. The failure of an egg to produce a viable offspring might be a function of a number of factors including genetic defects, disease and natural enemies (e.g. egg parasites and egg predators). Eggs may also succumb to rigors of the abiotic environment, such as desiccation or temperature extremes. A thorough knowledge of the success of eggs could aid

us in explaining the distribution and abundance of mantid species.

*Tenodera aridifolia sinensis* Saussure was introduced from Asia to the area of Philadelphia, Pennsylvania, in 1896 (Laurent 1898). It is extremely common in our area and extends north to southern New York State (Fox 1939a) and south to the Carolinas and Georgia (personal observation). This is the species most commonly available to organic gardeners (Ross 1984) as oothecae distributed by mail, which well may explain the breadth of its distribution. *Tenodera angustipennis* Saussure, another Asian species, was first found in Maryland in 1926 (Gurney 1950) and was established in Delaware by 1930 (Jones 1933). While common in our area, this species does not attain the large population sizes which we find for *T. a. sinensis*, and does not appear to have a very broad distribution. The third species,

*Mantis religiosa* Linnaeus, was introduced from Europe to the area of Rochester, New York, in 1899 (Gurney 1950). While common in most of the northeastern states and extending into Canada, the southern limit to its range appears to be in our area, where we find it in a limited number of sites. We have not found this species in southern Delaware or states to the south. All three species also are sympatric in China (Yan et al. 1981). In the present study we examine the egg ecology of these three introduced species of praying mantids from two separate field sites, where they co-occur in northern Delaware.

#### MATERIALS AND METHODS

The oothecae of the three species of praying mantids were collected in late April 1985 from the two old-field study sites. These sites, designated AG and CHRY (see site description in Hurd and Eisenberg 1989a) are separated by approximately 3 km. Each ootheca was weighed and placed in an individual container and kept in the laboratory at room temperatures (ca. 20–22° C) until nymphal emergence was complete. Nymphs were then counted and each ootheca was cut into ca. 1-mm sections with a razor blade and examined for the presence of unhatched eggs. The majority showed no signs of development and were classified as dead eggs, which either were not fertilized or died before development could take place. Others clearly had undergone development and often appeared to be fully developed nymphs; these were classified as dead nymphs. No evidence of egg parasitism was found.

For each species from each population, linear regressions were calculated for the number of nymphs emerging from each ootheca and the total number of eggs in each ootheca, on ootheca weights. The regression lines within species were compared with ANOVA (Snedecor and Cochran 1980). Ootheca weights, number of nymphs emerging, the two categories of unhatched eggs, total unhatched eggs, the total number

of eggs per ootheca, and the percentages of eggs which emerged were compared using *t*-tests between populations of the same species. The percentage data were arcsine-transformed prior to testing.

#### RESULTS

A detailed analysis of the oothecae of the three mantid species is presented in Table 1. While *T. a. sinensis*, the largest of the three species, produced the heaviest oothecae (column C) and the greatest number of emerging nymphs (Column D), the egg totals in oothecae (D + G) were remarkably similar for all three species (H). The major differences among the species were found in percent emergence and the apportionment of egg mortality (E, F, and I). Over 80% of *T. a. sinensis* eggs emerged as nymphs, while this value for *T. angustipennis* was about 70%, and 30% for *M. religiosa*. About 75% of the mortality in *T. a. sinensis* oothecae was accounted for as dead eggs. In *T. angustipennis*, egg mortality was about evenly divided between dead eggs and dead nymphs, while in *M. religiosa*, almost 95% of the mortality was dead eggs.

Differences between the two populations of each of the three species for ootheca weight, number of emerging nymphs, and total eggs in an ootheca varied consistently between the two habitats. For each species, for each of the above parameters, the values from the CHRY populations were always greater than those for the AG populations, and these differences were statistically significant (*t*-tests,  $P < 0.05$ ) in five of the nine possible comparisons (Table 1). Differences in the unhatched egg categories between populations did not show the same trend. No differences in percent emergence were found between sites for any species.

The regression analyses on ootheca weight for number of nymphs emerging and total eggs are given in Table 2. In all cases no significant differences were found between either the slopes or intercepts of the lines for comparisons between populations of the same species from the two different sites. In

Table 1. Analysis of the oothecae of three mantid species from sites CHRY and AG. Columns C through H are means with their standard errors (SE). N = sample size. *T*-tests were done to test differences in mean values between sites for each species. TS = *Tenodera a. sinensis*, TA = *T. angustipennis*, MR = *Mantis religiosa*.

A. Species-site	B. N	C. Wt. (g)	D. Emerging Nymphs	E. Dead Eggs	F. Dead Nymphs	G. Dead Totals	H. Total D + G	I. % Emergence
TS-AG	28	1.58	193.3	29.8	13.1	42.9	236.2	81.8
SE		.08	14.9	9.5	5.3	10.1	10.4	
TS-CHRY	15	2.05	264.3	36.3	9.1	45.3	309.7	85.4
SE		.13	23.6	14.5	2.6	14.2	15.3	
<i>t</i>		3.19	2.66	0.39	0.53	0.14	4.05	0.44
<i>P</i>		.003	.011	.70	.60	.89	.0002	.67
TA-AG	20	0.97	148.1	32.8	26.8	59.6	207.7	71.3
SE		.08	22.6	10.3	5.5	11.9	17.5	
TA-CHRY	21	1.14	186.4	33.0	28.4	61.4	247.9	75.2
SE		.05	19.7	13.6	5.8	13.7	9.6	
<i>t</i>		1.86	1.28	0.01	0.20	0.10	2.04	0.90
<i>P</i>		.07	.21	.99	.85	.92	.048	.38
MR-AG	15	0.81	65.5	172.9	3.9	176.8	242.3	27.0
SE		.09	21.4	21.2	1.9	20.8	14.3	
MR-CHRY	39	1.11	115.1	160.0	14.6	174.9	289.9	39.7
SE		.06	17.9	20.1	2.5	19.0	13.9	
<i>t</i>		2.57	1.56	0.37	2.56	0.06	1.97	1.14
<i>P</i>		.013	.12	.71	.013	.95	.054	.26

every case, using egg totals rather than just the number of emerging nymphs improved the fit of the regression lines (elevated  $r^2$  values, Table 2).

#### DISCUSSION

Our results show some clear differences among the three species and between populations of each species. The consistent nature of the variation between the two populations for mean oothecae weights, mean number of nymphs emerging and mean total eggs per ootheca, indicates a qualitative difference between the two habitats (Eisenberg et al. 1992). Since food limitation has been well documented for field populations of mantids (Eisenberg et al. 1981, Matura and Nagai 1983, Hurd and Eisenberg 1984, 1990, Hurd 1989, Fagan and Hurd 1991), we feel that the simplest explanation for the observed differences is that the AG populations of each species were more severely food limited than the CHRY populations. It seems unlikely that all three species have

distinct genetic ecotypes in two nearby habitats. The notion that food limitation rather than some edaphic or genetic factor was responsible for the observed differences between sites is supported by two other lines of evidence: 1) the similarities of the regression lines between sites for numbers of nymphs emerging, on ootheca weight, and 2) the similarity in the proportions of egg mortality in each category for each species. Also, in an earlier work (Eisenberg and Hurd 1977) we reported on the emergence characteristics of a mixed collection of *T. a. sinensis* oothecae from various sites. Combining the data from the two *T. a. sinensis* populations in our present study and comparing the resultant regression line with that of Eisenberg and Hurd (1977) for number of nymphs emerging on ootheca weight shows no significant difference in either slope ( $F_{1,69} = 1.50, P > 0.05$ ) or intercept ( $F_{1,70} = 0.02, P > 0.05$ ). In fact, the 1977 regression predicted 5148 nymphs of the 5413 which actually emerged in the present study. The



Table 2. Regression analyses for the number of nymphs emerging and total eggs on ootheca weight for three species from sites CHRY and AG. Symbols as in Table 1.

Species	Location	Regression Values		r <sup>2</sup> (%)
		Intercept	Slope	
TS	CHRY	-24.62	140.68	60.16 (nymphs)
		87.59	108.12	84.13 (total eggs)
TS	AG	-1.89	123.86	49.58 (nymphs)
		72.14	104.10	71.66 (total eggs)
TA	CHRY	-78.20	230.49	39.07 (nymphs)
		74.14	151.31	70.97 (total eggs)
TA	AG	-86.44	242.29	77.49 (nymphs)
		6.77	207.57	94.60 (total eggs)
MR	CHRY	-58.04	152.30	39.15 (nymphs)
		121.57	151.34	48.89 (total eggs)
MR	AG	-76.98	172.63	38.52 (nymphs)
		142.34	123.25	57.45 (total eggs)

constancy of this relationship over time and space argues against intrinsic differences among populations and also indicates that, at least for *T. a. sinensis*, emergence behavior in our area is rather consistent from year to year and that oothecae weights are good predictors of numbers of emerging nymphs.

One way to examine hatching success is to compare the distance between regression lines for numbers of eggs and numbers of hatched nymphs across ootheca weights. For example, the relative constancy of hatching success between the two habitats held even for *M. religiosa*, which had the poorest success of the three species. The difference between numbers of emerging nymphs and numbers of eggs was relatively large, but varied neither between sites or among ootheca weights (Fig. 1). Therefore, the nutritional success, or lack thereof, of a parent female does not affect the probability that her eggs will hatch. This guarantees the decoupling of individuals across generations, such that a newly hatched nymph is neither advantaged or disadvantaged by its parents' environment.

What remains unexplained is the reason for the relatively low percent emergence observed for *M. religiosa* in this study, less than half the values reported for 1986 by

Eisenberg et al. (1992). Since hatching success was approximately equally low for both sites, this would seem to indicate that the poor emergence of *M. religiosa* was due to regional abiotic factors (temperature, humidity, etc.) which can vary among years. The eggs of *M. religiosa* require exposure to cold in order to terminate diapause (Salt and James 1947). This may limit their southern distribution to those regions in which the winters are long and cold enough to allow completion of diapause. Thus, the difference between the regression lines for emerging nymphs and total eggs (Fig. 1) may well be a reflection of insufficiently low temperatures during winter in northern Delaware. If so, we predict that this difference and the variation therein between years would decline closer to the center of this species' geographic distribution (e.g. New York State).

Fall-collected oothecae of both *Tenodera* species routinely are hatched in our laboratory without being subjected to cold, which makes it easy to run laboratory studies the year round. In fact, this can be a problem in the southern portion of their distribution; we have seen eggs of *T. a. sinensis* hatch in October in North Carolina, which assures that the nymphs will be killed by frost long before they can mature. Therefore, in Del-

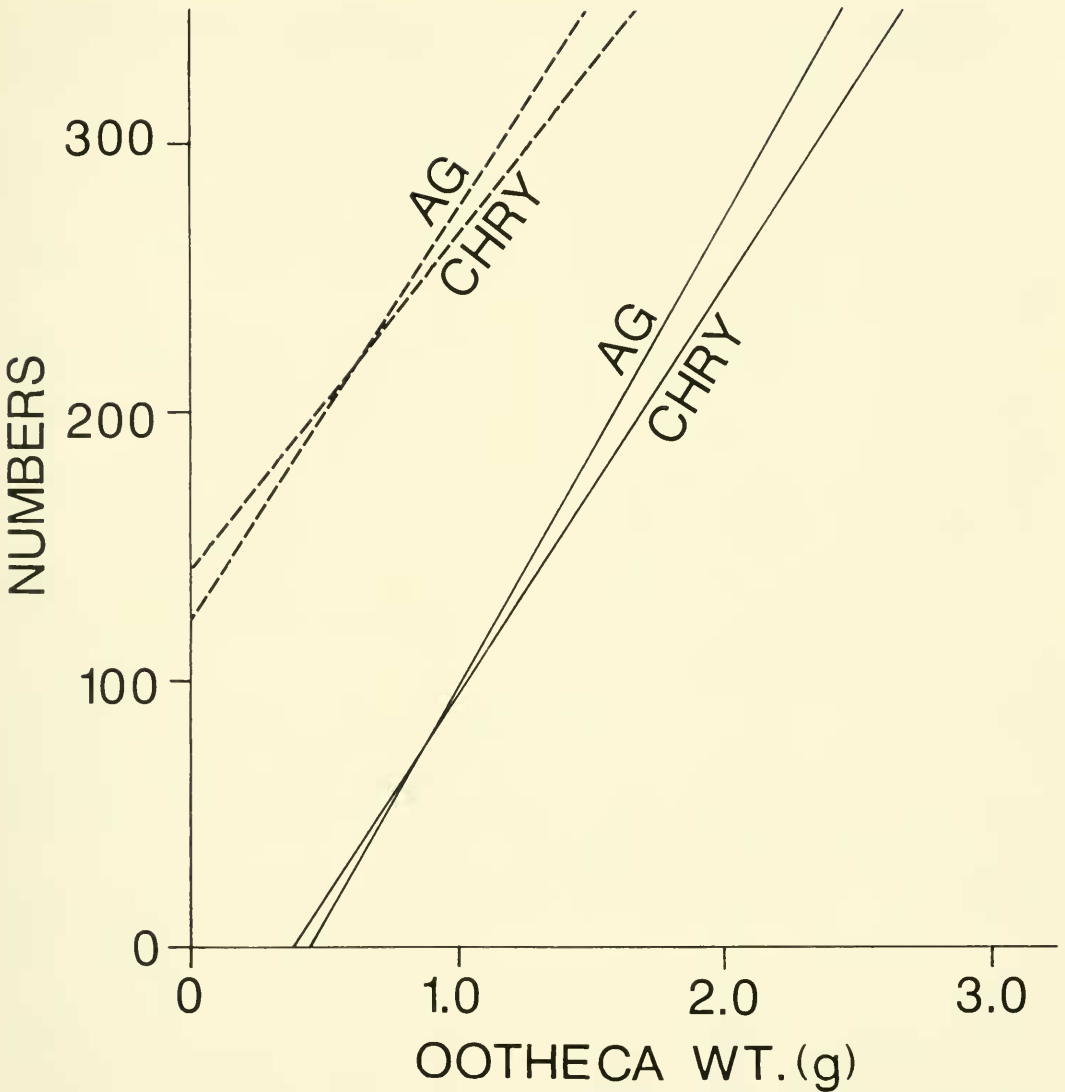


Fig. 1. Regression lines for numbers of nymphs emerging (solid lines) and total numbers of eggs (dashed lines), on oothecae weights for *Mantis religiosa* (see Table 2 for regression summary statistics). CHRY and AG are the two different field sites (see text).

aware the earlier oviposition takes place in the fall the earlier eggs are likely to hatch the following spring, so that asynchronous oviposition may at least partially explain the asynchrony in emergence times for these two species (Hurd and Eisenberg 1989b). Asynchronous emergence can translate into differences in life history stage within a population which may persist throughout the

season (Hurd and Eisenberg 1989a), and induce cannibalism among co-occurring nymphs of different stadia (Hurd 1988).

Both fecundity and egg mortality are important components of population growth. Although fecundity in mantids has been linked to food supply (Matsura and Moorooka 1983, Eisenberg et al. 1981, Hurd 1989), egg mortality apparently is not. Our

results implicate abiotic mortality factors; however, natural enemies may be important in some cases. In the present study and in an earlier one (Eisenberg et al. 1992) we found no evidence for any egg mortality caused by natural enemies. Fox (1939b) found the egg parasite *Podagrion mantis* in about 4% of the oothecae of both *T. angustipennis* and *T. a. sinensis* in collections from Cape May County, New Jersey, and we have seen this parasite in *T. angustipennis* oothecae from southern Delaware. A high incidence of egg parasitism by *P. mantis* in our native mantid, *Stagmomantis carolina*, was reported by Girault (1907) and Rau and Rau (1913), and Fox (1939b) speculated that low incidence of *P. mantis* in *T. angustipennis* was due to its recent introduction and the lack of overlap of its range with *S. carolina*. It is interesting to note that more than 50 years after Fox's work, mantids in northern Delaware still are free of this egg parasite.

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